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SURVIVORSHIP OF WOLF SPIDERS (LYCOSIDAE) REARED ON DIFFERENT DIETS

George W. Uetz, Jennifer Bischoff, and **Joseph Raver:** Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221-0006 USA

ABSTRACT. Observations from previous studies have indicated that lycosid spiders often die before maturing when raised on only one prey type. Two wolf spider species (*Lycosa helluo* collected from Florida, and *Lycosa* sp. collected from Kentucky) were used to test the hypothesis that diet affects survivorship. Siblings from one egg sac of each species were divided into two groups of 50 spiderlings each, and reared under identical conditions with different diets. The polytypic diet consisted of crickets (*Acheta domesticus*), fly grubs (*Sarcophaga bullata*), cockroaches (*Periplaneta americana*), mealworms (*Tenebrio molitor*), beetles (*Dermestes* sp.), and an occasional supplemental orthopteran collected from the field. The monotypic diet consisted only of crickets (*A. domesticus*). There was significantly lower survivorship of spiders raised on monotypic prey in both species, although the pattern of mortality over time varied between species. There were also significant differences in certain body size parameters (cephalothorax width, total leg I length, patella-tibia length) measured at maturity between spiders raised on polytypic or monotypic diets in one species (*L. helluo*). In addition, *Lycosa helluo* raised on polytypic diets reached sexual maturity earlier than those reared on monotypic prey. These results suggest that there are fitness-related eonsequenees of dietary breadth in spiders, and support the hypothesis of Greenstone (1979) that lycosids require a mixed diet.

INTRODUCTION

The dietary breadth of generalist predators, including spiders, is usually thought to indicate a strategy of opportunistic prey capture (Riechert & Luczak 1982, Riechert & Lockley 1984, Riechert & Harp 1987; Uetz 1990, 1992). However, there is growing evidence that many animals (especially herbivores) maintain a mixed diet for nutritional reasons (Belovsky 1978; Slansky & Rodriguez 1987). Greenstone (1978) found that lycosid spiders (*Pardosa ramulosa* (McCook)) did not switch to more abundant or profitable prey items as prey density changed. Optimization of critical nutritional requirements (amino acids, fatty acids, etc.) may be why lycosids maintain a mixed diet in the field despite high abundance of single prey species (Greenstone 1979).

Observations from a number of previous studies have indicated that lycosid spiders often die before maturing when raised on a diet composed of only one prey type (Miyashita 1968; Van Dyke & Lowrie 1975; C. D. Dondale, J. S. Rovner, pers. comm.). This may be true for other spider families as well (e. g., Agelenidae – Riechert & Harp 1987; Linyphiidae – D. H. Wise, pers. comm.). In particular, juveniles raised on a diet of *Drosophila melanogaster* do not survive past the 4th or 5th instar (Van Dyke & Lowrie 1975; K. Redborg, pers. comm.), suggesting the possible absence of critical nutrients in this prey species. In contrast, reduced survivorship was not seen in rearing studies with lycosids and other spider families where a variety of insect species were available as prey (Eason 1969; Peck & Whitcomb 1970). In this study, we tested the influence of diet on survival and development of lycosids through adulthood by rearing spiders under identical controlled conditions, but feeding them on polytypic and monotypic diets.

METHODS

Two species of lycosid spiders were used in this study: *Lycosa helluo* Walckenaer, collected from Highlands Hammock State Forest in Highlands County, Florida, and *Lycosa* sp. (possibly an undescribed member of the *L. helluo* group), collected from a power line right-of-way along the Licking River in Kenton County, Kentucky. Females of each of these species, carrying egg sacs, were collected and brought into the laboratory.

After emergence of spiderlings, and dispersal from the female's abdomen, 100 siblings from each species were separated from the female and assigned at random to experimental groups of 50 spiderlings each. Spiderlings were reared at first

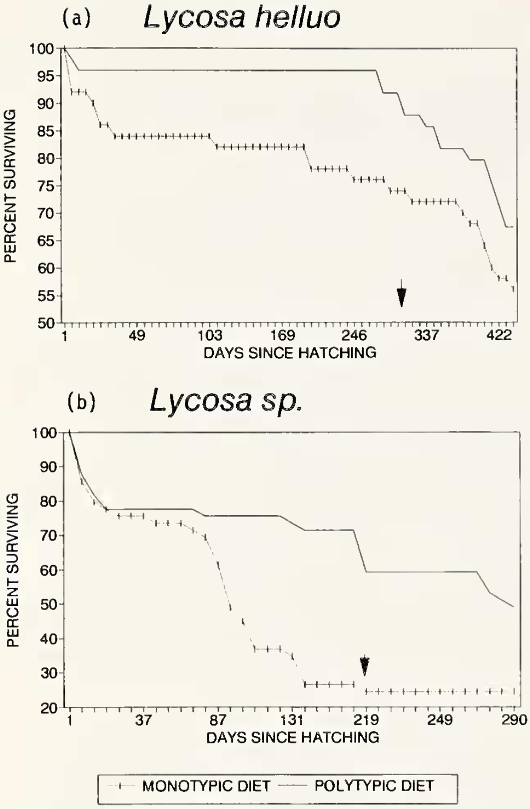

Figure 1.—Survivorship (in days) of laboratory populations of lycosids raised on different diets. Solid line—polytypic diet; dashed line—monotypic diet. Arrows indicate approximate earliest onset of sexual maturity. *a: Lycosa helluo* from Florida; *b: Lycosa* sp. from Kentucky.

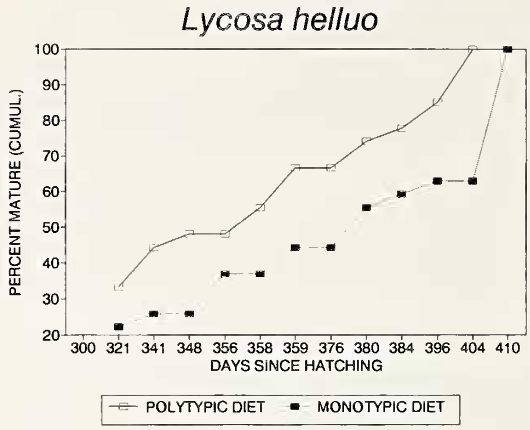

Figure 2.—Cumulative (percent) maturation curves for laboratory populations of *Lycosa helluo* from Florida raised on different diets. Open squares/solid line—polytypic diet; filled squares/dashed line—monotypic diet.

in 10 cm long, 1 cm diameter glass tubes with cotton plugs at each end, then transferred to semi-clear cylindrical plastic containers (11.8 cm high, 15.3 cm diameter). Rearing conditions for spiders were identical except for diet: 12:12 hr light/dark cycle, constant 27 °C temperature, relative humidity 65–75%. Water was available *ad libitum* in rearing containers from soaked cotton plugs and/or small shell vials with water and a cotton plug at one end.

Insect prey (three to five individuals selected for size approximately ten percent less than spider size) were provided twice weekly. The polytypic diet consisted of crickets (*Acheta domesticus* (L.)), flesh fly grubs (*Sarcophaga bullata* Park), cockroaches (*Periplaneta americana* (L.)), mealworms (*Tenebrio molitor* L.), beetles (*Dermestes* spp.) and occasional orthopterans (Tettigoniidae, Acrididae) collected from the field. The monotypic diet consisted only of crickets (*Acheta domesticus*).

Spider survival was monitored with each feeding, or at least once weekly, throughout development until sexual maturity. Molts were recorded when exuviae were observed in the container. At approximately four weeks after reaching sexual maturity, a subsample of surviving female spiders from each experimental group was weighed and measured. Body size parameters measured included body length (BL), cephalothorax width (CW), abdomen width (AW), total leg length (TLL) of one leg I (chosen at random), patella-tibia length (Pa-Ti) of that same leg, and live weight.

RESULTS

In both species, differences in survivorship were apparent between experimental groups (Figure 1a, b). These differences between monotypic and polytypic prey treatments are significant (Kolmogorov-Smirnov test: D_{max} values = 0.41 (*L. helluo*); 0.37 (*Lycosa* sp.); $P < 0.001$ for both). Patterns of survivorship varied between species, as mortality occurred at different rates and at different times of the life cycle. In *L. helluo*, differential mortality was apparent in the first 30 days (Fig. 1a). For *L. helluo* fed a polytypic diet, approximately 96% of spiders survived past 250 days, and about 85–90% reached sexual maturity. The mortality rate (no. dying/no. alive at start × 100) for this treatment was 12.2%. For

Table 1.—Body size measurements of adult female wolf spiders fed on different diets.

	Body size parameter					
	BL (mm)	CW (mm)	AW (mm)	TLL (mm)	Pa-Ti (mm)	Weight (g)
Lycosa helluo						
Monotypic diet:						
Mean	27.09	9.64	10.27	30.69	10.85	1.73
SD	1.32	0.84	1.27	2.67	0.85	0.22
n	18	18	18	17	17	17
Polytypic diet:						
Mean	27.80	10.26	10.21	32.87	11.67	1.79
SD	1.34	0.79	1.15	2.69	0.89	0.22
n	13	14	15	12	15	12
t-test	1.42	2.02	0.14	2.07	2.58	0.71
P value	ns	<0.05	ns	<0.05	<0.05	ns
Lycosa sp.						
Monotypic diet:						
Mean	20.32	8.00	7.89	23.05	9.41	0.69
SD	0.75	0.36	0.51	1.95	0.81	0.09
n	6	5	6	6	6	6
Polytypic diet:						
Mean	21.07	7.68	8.33	22.04	8.81	0.81
SD	1.51	0.41	0.57	2.06	0.77	0.14
n	11	9	11	11	11	11
t-test	1.07	1.46	1.49	0.92	1.39	1.7
P value	ns	ns	ns	ns	ns	ns

L. helluo fed a monotypic diet, survivorship was fairly constant after the initial decline, but only 75% reached sexual maturity (the mortality rate for this treatment was 28%). These results contrast sharply with survivorship patterns of *Lycosa* sp. (Fig. 1b); both treatment groups for this species experienced a 25% decline in survivorship in the first 30 days. Survivorship curves for *Lycosa* sp. diverged after approximately 80 days, with only 25% of the spiders reared with a monotypic diet surviving to adulthood. The mortality rate for the monotypic treatment was 75.5%. In contrast, >70% of those reared on a polytypic diet survived to adulthood (a mortality rate of 28.5%).

Owing to difficulty in observing female genitalia on live specimens, precise data on age at sexual maturity were only available for *L. helluo* (Fig. 2). Distributions of maturation times were significantly different for the two diet treatments (Kolmogorov-Smirnov test: $D_{max} = 0.37$; $P < 0.05$). Spiders raised on a polytypic diet reached sexual maturity earlier than those raised on a monotypic diet; differences in age at maturity are significant (Mann-Whitney *U*-test: $U_s = 482$; $P < 0.05$). The median age at maturity for polytypic diet treatment individuals was estimated to be 337 days; for monotypic diet treatment individuals, 387 days (precise dates could not be determined in all cases, as spiders were monitored on a weekly basis).

Body size parameters measured at maturity were significantly different between experimental treatments for one of the two species studied (Table 1). For *L. helluo*, significant differences between treatments were seen in cephalothorax width (T = 2.02; $P < 0.05$), total leg length (T = 2.07; $P < 0.05$); and patella-tibia length (T = 2.58; $P < 0.05$), with spiders raised on polytypic diets larger in all measures. In contrast, for *Lycosa* sp., no significant differences in body size parameters were seen (although lowered survival and consequent smaller sample sizes may have influenced this result).

DISCUSSION

Results of this study provide strong support for earlier hypotheses regarding the importance of a mixed diet for lycosid spiders and other spider species (Peck & Whitcomb 1970; Greenstone 1979; Riechert & Harp 1987). It is important to note that the monotypic diet used in this study was composed of a domesticated prey animal, which was itself reared under artificial conditions with an unknown diet. It is possible that the diet fed to crickets in culture may have lacked a nutrient requirement critical for spiders (although not for crickets), and an experimental study with a monotypic diet of field-collected crickets might have yielded a different result. Walcott (1963) reported that *Achaearanea tepidariorum* (Koch) had poor survivorship when fed mealworms whose diet was limited to standard mealworm bran. However, when mealworms were fed vitamin-enriched commercial bran cereals, spider survivorship was improved dramatically. This result may also explain why lycosids suffer high mortality when fed on a diet of *Drosophila*, an insect known to lack a requirement for linoleic and linolenic acid in its diet (K. Redborg, pers. comm.). While these findings clearly suggest that rearing of spiders in the laboratory could be enhanced by providing a variety of prey species, it also raises questions about the role of dietary mixing in the field.

The differences in survivorship, age at maturation, and size at maturity seen in this study between spiders fed on a polytypic versus a monotypic diet suggest that there are clear fitness consequences of dietary breadth. Differential mortality rates, with approximately 2.3–2.6 times greater mortality for spiders fed a monotypic diet, suggest that selection pressure for dietary mixing could be strong. Although in this study all other factors were controlled, the lack of dietary mixing might affect spiders in the field in other ways as well. For example, if physical condition were affected by dietary breadth, differences in vulnerability to predation and parasitism might result. Moreover, earlier maturation and larger size at maturity might well confer other fitness advantages on spiders with mixed diets (Uetz 1992). It is well known that larger spiders are more likely to win contests over territory and or mates (Austad 1983; Christenson 1984; Suter & Keiley 1984; Riechert 1986; Uetz & Hodge 1990). Spiders maturing early in the breeding season might have access to more potential mates, and have a longer time to feed before laying eggs. In addition, offspring of spiders breeding earlier might have a competitive size advantage over other broods, and might even cannibalize them (Edgar 1969).

This demonstration of differential mortality and other fitness-related consequences of diet provides strong support for the hypothesis that dietary mixing is adaptive in spiders (Greenstone 1979). While the proximate mechanisms by which spiders maintain a mixed diet remain unclear, there is new evidence that foraging behaviors affecting diet choice in spiders are genetically-based (Hedrick & Riechert 1989; Riechert 1991), and therefore potentially subject to selection. As spiders are considered important model organisms for research in ecology and behavioral genetics, as well as potential agents of agricultural pest management (Wise 1984; Riechert & Lockley 1984; Uetz 1992), further study of the adaptive significance of diet in these animals deserves attention.

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